RESEARCH ARTICLE

Planting Seedlings in Tree Islands Versus Plantations as a Large-Scale Tropical Forest Restoration Strategy

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Abstract

Planting tree seedlings in small patches (islands) has been proposed as a method to facilitate forest recovery that is less expensive than planting large areas and better simulates the nucleation process of recovery. We planted seedlings of four tree species at 12 formerly agricultural sites in southern Costa Rica in two designs: plantation (entire 50 × 50 m area planted) and island (six patches of three sizes). We monitored seedling survival, height, and canopy area over 3 years. To elucidate mechanisms influencing survival and growth, we measured soil and foliar nutrients, soil compaction, and photosynthesis. Survival of all species was similar in the two planting designs. Seedling height and canopy area were greater in plantations than islands at most sites, and more seedlings in islands decreased in height due to damage incurred during plot maintenance. Survival, height, and canopy area were both site- and species-specific with the two N-fixing species (*Inga edulis* and *Erythrina poeppigiana*) greater than the other species (*Terminalia amazonia* and *Vochysia guatemalensis*). Foliar N was higher in *Terminalia* and *Vochysia* in sites where *Inga* growth was greater. Soil nutrients, however, explained a small amount of the large differences in growth across sites. Leaf mass per area was higher in islands, and P use efficiency was higher in plantations. Our results show advantages (good seedling survival, cheaper) and disadvantages (more seedling damage, slightly lower growth) to the island planting design. Our study highlights the importance of replicating restoration strategies at several sites to make widespread management recommendations.

Key words: Costa Rica, nucleation, premontane forest, reforestation, seedling growth.

Introduction

Planting tree seedlings is a common restoration strategy and is often successful in accelerating tropical forest recovery (e.g. Parrotta & Knowles 2001; Cusack & Montagnini 2004; Lamb et al. 2005). If seedlings provide canopy cover they can overcome many barriers to forest regeneration in degraded tropical sites (e.g. increasing seed rain, ameliorating microclimatic extremes, shading out pasture grasses), and thus facilitate the natural establishment of a diversity of forest species (reviewed in Holl 2002b). This strategy can be expensive, however, especially when large areas are restored (Parrotta & Engel 2001; Rodrigues et al. 2009).

A few studies have tested planting trees in patches or "islands" (Robinson & Handel 2000; Zahawi & Augspurger 2006; Rey Benayas et al. 2008) rather than as plantations. This practice mimics the natural nucleation process (Yarranton & Morrison 1974) in which primary colonists establish in patches and spread outward clonally and/or by facilitating the colonization of later-successional species. This process has been widely documented for remnant trees and shrubs in tropical old fields (e.g. Guevara et al. 1992; Vieira et al. 1994; Holl 2002a; Schlawin & Zahawi 2008). If seedlings planted in islands show similar survival and growth to plantations and facilitate the establishment of other plant species (Zahawi & Augspurger 2006; Cole et al. in press), then island plantings may be a more cost-effective restoration strategy. However, the two approaches have never been compared rigorously.

Most past tropical forest restoration studies have been restricted to a single or a few sites (e.g. Cusack & Montagnini 2004; Carpenter et al. 2004a; Siddique et al. 2008). The few studies conducted at multiple sites (Piotto et al. 2003; Calvo-Alvarado et al. 2007; Wishnie et al. 2007) or blocks within sites (Carpenter et al. 2004a) show that seedling growth rates can be highly variable, even on a small scale. Accordingly, it is not often possible to extrapolate results to a regional level, and the high variability underscores the importance of testing restoration strategies at multiple sites to clarify the mechanism(s) underlying differences in seedling growth.

Tropical seedling growth in abandoned agricultural lands is limited by numerous factors including soil physical and chemical conditions, competition with existing vegetation, and microclimatic conditions (reviewed in Holl 2002b). Designing

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effective restoration strategies requires a detailed understanding of species traits and resource-use patterns, as well as knowledge of site characteristics. For example, examining species' responses to light and nutrients, provides insight into the ability of a species to tolerate stress (Palmer et al. 2006).

The goal of this study was to compare survival and growth of tree seedlings planted in plantations and small patches (islands) as a strategy to facilitate tropical forest recovery. To test this restoration approach, we evaluated the growth and development of four tree species planted in two designs: plantation (entire 50×50 m area planted) and island (six patches of three sizes planted within the 50×50 m area). To test planting approaches on lands representative of agricultural landscapes and make results generalizable at a regional level, we replicated the experiment at 12 sites across a 100 km^2 area in southern Costa Rica. We collected additional data on soil nutrients, soil compaction, and photosynthesis to better understand the mechanisms underlying species and site differences. We anticipated that seedling survival and growth would be similar in plantations and islands given the identical species mixes and similarly open conditions, and that growth would vary across sites depending on soil conditions.

Methods

Study Region

This study was carried out from June 2004 to July 2008 at 12 sites separated by 0.7–8 km and located near the town of Agua Buena (8° 44′ 36″ N, 82° 58′ 04″ W) and the Las Cruces Biological Station (8° 47′ 7″ N, 82° 57′ 32″ W) in Coto Brus County, Costa Rica. Sites are in the tropical premontane rain forest zone (Holdridge et al. 1971), range in elevation from 1,060 to 1,430 m asl (Table 1), and receive mean annual rainfall of circa 3,500 mm with a dry season from December to March. Mean annual temperature is approximately 21°C. Like much of Central America, the landscape is a highly fragmented mosaic of mixed-use agricultural fields and forest patches.

All sites had been used for ≥18 years for agriculture and most were burned once or twice after clearing, but not thereafter. Sites were either recently abandoned pastures generally dominated (>80% cover) by one or a combination of three exotic forage grasses, *Axonopus scoparius* (Flüggé) Kuhlm., *Pennisetum purpureum* Schumach., and *Urochloa brizantha* (Hochst. Ex. A. Rich.) R. D. Webster, or coffee farms dominated by a mixture of forage and non-forage grasses, forbs, and the fern *Pteridium arachnoideum* (Kaulf.) Maxon (Table 1). Most sites are steeply sloping (15–35°) with a few sites on flatter terrain (5–10°). Sites spanned a range of aspects.

Study Species

To evaluate tree planting strategies that could be broadly used to facilitate tropical forest recovery, we chose species that (1) have high survival (>80%), rapid growth (1–2 m yr^{-1}), and extensive canopy development in the first few years after planting (Nichols et al. 2001; Carpenter et al. 2004a; Calvo-Alvarado et al. 2007); (2) are readily available in local nurseries; and (3) are widely used in agroforestry, restoration, or plantations in Central America. Two species, *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae), produce valuable timber and support establishment of native woody species in their understory (Cusack & Montagnini 2004). Two species, *Erythrina poeppigiana* (Walp.) Skeels and *Inga edulis* Mart. (both Fabaceae), are fast growing, N-fixing species that have extensive branching architecture and fruit (*Inga* only) that attract birds (Pennington & Fernandes 1998;

Table 1. Elevation, year planted, initial vegetation, and site use history for the 12 study sites.

Site	Elevation (m asl)	Year Planted	Dominant Vegetation at the Time of Planting	Site Use History
AC	1,430	2005	*Axonopus scoparius*	Corn and beans (4 yr), fallow (12–14 yr), pasture (13 yr)
BB	1,290	2004	Mixture of grasses and forbs	Pasture (10 yr), coffee (32 yr)
BR	1,060	2004	*Urochloa brizantha*	Coffee (35 yr), pasture (20 yr)
CD	1,160	2004	*U. brizantha* and *Pennisetum purpureum*	Coffee (16 yr), pasture and orange trees (2 yr)
GN	1,170	2005	*A. scoparius*	Pasture (47 yr)
HB	1,120	2005	*A. scoparius*	Coffee (25 yr), pasture (8 yr), fallow (4 yr)
JG	1,180	2005	Mixture of grasses and forbs	Mixed simultaneous uses: mostly beans (35 yr) and fallow (5 yr), partly coffee (30 yr) and pasture (10 yr)
LL	1,160	2004	*P. purpureum*	Pasture (17 yr), vegetables (5 yr), coffee (7 yr), beans (5 yr), fallow (15 yr)
MM	1,100	2004	*P. purpureum*	Pasture (>40 yr), fallow (4 yr)
OM	1,120	2005	Mixture of grasses and forbs	Beans and corn (10 yr), pasture (5 yr), coffee (5 yr), fallow (5 yr)
RS	1,190	2004	Mixture of grasses and forbs	Mixed simultaneous uses: mostly pasture (10 yr), coffee (20 yr), corn and beans (2 yr), partly intermittently grazed pasture (20 yr)
SG	1,110	2004	*U. brizantha*	Coffee (25 yr), fallow (3 yr), pasture (4 yr)

Land-uses are based on land owner interviews. Land-uses are listed chronologically from earliest to most recent with estimated times of each land use.

Nichols et al. 2001; Jones et al. 2004). Both are native to Latin America but not to Costa Rica and are used widely in inter-cropping systems to provide shade and increase soil nutrients. Species are referred to by their generic names throughout.

Experimental Layout

Each site had two 50×50 m planting designs (island and plantation) in which seedlings of the four tree species were planted in June–July 2004 or 2005 (Table 1). In island plots, trees were planted in six patches separated by a min-imum of 8 m: two small (five seedlings each), medium (13 seedlings each), and large patches (25 seedlings each). In plantation plots, seedlings were planted throughout the 50×50 m plot (313 seedlings; Fig. 1). In both island and plantation plots, seedlings were planted in alternating rows of *Terminalia/Vochysia* and *Erythrina/Inga*. Species were planted alternately 4 m apart, and rows were separated by 2 m and offset by 2 m so that seedlings were separated by 2.8 m (Fig. 1).

Seedlings were acquired from a local nursery and were approximately 20–30 cm tall when planted. Following stan-dard forestry practices in the region (J. Calvo 2003, Insti-tuto Tecnológico de Costa Rica, personal communication), seedlings received a single 50-g application of slow-release 10:30:10 NPK fertilizer, as well as a 5-g application of a nematicide (Mocap). Seedlings that died within the first 2 years after planting were replaced. *Vochysia* was not planted until the second year at two sites (BR and LL) due to an insufficient number of seedlings, so these were not included in analyses. All plots were cleared of above-ground woody vegetation with machetes prior to planting and at approxi-mately 3-month intervals for 2.5 years to allow seedlings to grow above existing vegetation.

Data Collection

We measured seedling height immediately following plant-ing and survival and height on an annual basis (June–July) for 3 years; 3 years after planting we measured canopy area. Canopy area was calculated as an ellipse ($\pi d_1 d_2/4$) using the canopy diameter of two perpendicular axes measured to the nearest 5 cm. We recorded survival of all seedlings. We mea-sured height and canopy area of all seedlings in island plots and approximately one-third of seedlings (randomly selected) in plantations to equalize the number of measured seedlings across planting designs.

In August 2007, we collected twenty-five 2.5-cm diameter $\times$ 15-cm deep soil cores across each plot. Cores were mixed, passed through a 2-mm sieve, air dried, and analyzed for organic matter, Bray and Mehlich III P, and cations and micronutrients using Mehlich III extractions following stan-dard procedures at Brookside Laboratories, Knoxville, Ohio (see www.blinc.com/worksheet_pdf/SoilMethodologies.pdf and Gavlak et al. 2003 for details on protocols). A small sample was finely ground, and C and N were determined by Dumas combustion using a Carlo Erba 1108 elemental analyzer at the University of California, Santa Cruz Stable Isotope Labora-tory. In 2008, we collected five soil bulk density cores (5-cm diameter $\times$ 10-cm deep) across each plot. We dug a hole to expose a vertical face, inserted a metal putty knife at 10-cm depth to ensure that we sampled the correct volume, and then inserted a thin-walled metal cylinder. Bulk density samples were dried at $105°$C for ≥ 48 hours and weighed.

During July 2008, we collected leaves from six randomly selected trees per species in each planting design for foliar nutrient analyses. For each tree, approximately 3–8 fully expanded, young leaves were harvested and samples were bulked across individuals of each species in a plot. Leaf area was determined using a LI-COR 3100 leaf area meter
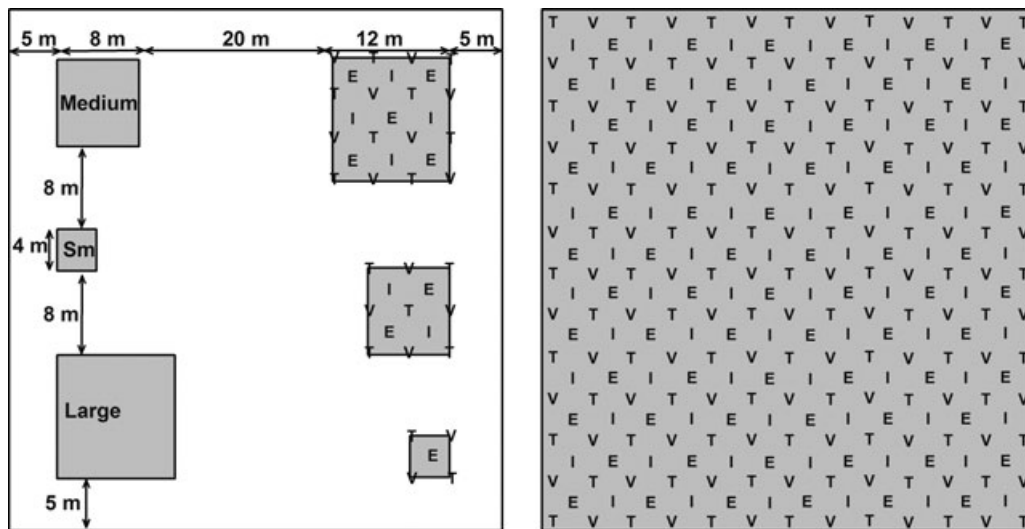

Figure 1. Planting arrangement and island size classifications for island (left) and plantation (right) plots (50×50 m) at one restoration site. Large islands are 12×12 m, medium islands are 8×8 m, and small islands are 4×4 m. Shaded areas are planted with trees. Trees are indicated by letters: *Erythrina* (E), *Inga* (I), *Terminalia* (T), and *Vochysia* (V). Nonshaded areas are nonwoody vegetation, primarily grasses and forbs. Sm = small island.

(LI-COR, Lincoln, NE, U.S.A.). Tissue was dried at 65°C for 48 hours and weighed to calculate leaf mass per area (LMA). Samples were ground and analyzed for leaf nutrients at Brookside Laboratories. Nitrogen was measured on dry ground samples by combustion on an elemental analyzer. Other nutrients were analyzed on a Thermo Jarrell Ash ICP (Thermo Fisher Scientific, Waltham, MA, U.S.A.) after microwave digestion with nitric acid and hydrogen peroxide (Gavlak et al. 2003).

We measured maximum rates of photosynthesis and light response curves using a LI-COR 6400 IRGA Portable Photosynthesis System at six sites (BR, CD, GN, JG, OM, and SG). Measurements were taken between 0800 and 1400 hours, at approximately 70–75% relative humidity, 400 μmol m^{-1} s^{-1} CO_2 concentration, and 1,200 μmol m^{-2} s^{-1} light. At each site, we measured three fully expanded canopy leaves on four trees of each species in plantations and large islands.

Given their time intensity, light response curves were measured at two sites (GN, JG). We measured one leaf on two individuals per species in each planting design ($n = 4$/species/ site). Light response of net photosynthesis was measured at nine light levels decreasing from 2,000 to 0 μmol m^{-2} s^{-1}; at each light level leaves were equilibrated for approximately 10 minutes before recording photosynthesis. Quantum efficiency, light saturation points, and light compensation points were estimated for each species based on the mean of the two leaves using Photosyn Assistant (Dundee Scientific, Dundee, UK), which determines these parameters by fitting the light response data to a quadratic model function (Prioul & Chartier 1977). We estimated variables using least squares fitting regression and the Nelder-Mead minimization routine (Nelder & Mead 1965). Instantaneous photosynthetic nitrogen- and phosphorus-use efficiency were calculated as $A_{mass(max)}$/ N_{mass} or $A_{mass(max)}$/P_{mass}.

Data Analysis

We calculated percent survival and height change (height in year n−height *initial*) and canopy area in year 3 at the plot level. Seedlings that died and were replaced, as well as seedlings that decreased in height by >10 cm from 1 year to the next, were excluded from height change and canopy analyses to analyze growth separately from damage to seedlings. In most cases, height reduction was caused by an inadvertent machete strike during plot clearings, although in some *Erythrina* the main meristem died, likely due to shoot boring insects (Araya et al. 1992). It was impossible to consistently record all seedlings that were damaged during the clearing process, because some died and were entirely missing at the time of annual measurements. Accordingly, we calculated the percentage of surviving seedlings with decreasing height, although this underestimated the number of damaged seedlings.

The experiment was setup as a randomized complete block design with site as the blocking factor. We used a mixed-model analysis of variance (ANOVA) to analyze the effect of planting design and species (fixed factors) and site (random factor) on percent survival, canopy area, height change in year 3, and individual leaf foliar nutrients; we included all three individual factors and two-way interactions in the model. Preliminary repeated measures analysis on height change indicated that trends across species, planting designs, and sites were generally consistent and became stronger over time. Therefore, we focused on year 3 data to evaluate the effectiveness of these planting strategies. We analyzed data by site rather than by year planted as the variance in survival and growth among sites planted in the same year was much greater than between sites planted in 2004 and 2005; moreover, the range of values across sites was similar in both years. The same model was used to compare height and canopy area in the third year between seedlings that were planted on the "edge" (in the two rows at the exterior of the plantation) and for seedlings planted in the "interior" of the plantation (Fig. 1). Because there were few seedlings in small islands, we combined data from small and medium islands and conducted analyses for all species pooled. We used a paired *t*-test to compare survival and height change of seedlings in different island sizes.

We compared soil nutrients between island and plantation plots within a site using paired *t*-tests. We tested the relationship of height and canopy area to soil and foliar nutrients, as well as slope, aspect, and elevation, using Spearman rank correlation coefficients. Given the large number of correlations, we corrected the level of significance for multiple comparison following Benjamini and Hochberg (1995), which reduces type I errors but has higher power than Bonferroni adjustments (Verhoeven et al. 2005).

Percentage variables were arcsine square root transformed and some variables were log transformed or ranked to meet assumptions of normality and homogeneity of variances. We report means ± 1 SE throughout and all analyses were done using SAS 9.1.3.

Results

Seedling Survival and Growth

Of the 4,788 seedlings planted, 88.1% survived through the first year, 95.2% survived through the second year, and 96.5% in year 3. There were strong species ($F = 11.7$, $p \leq 0.0001$) and species × site interaction effects ($F = 2.5$, $p = 0.0075$) on survival, whereas there was no effect of planting design ($F = 0.02$, $p = 0.8807$), nor were other interaction terms significant ($p > 0.05$). Percent survival (Fig. 2a) was highest in *Inga* (90.7–98.8% across sites), intermediate in *Erythrina* (58.0–96.5%), and lowest in *Vochysia* (23.0–97.4%) and *Terminalia* (46.5–90.3%). *Terminalia* and *Vochysia* survival were much lower at one site (AC) than any others.

A larger percentage of surviving seedlings decreased in height by >10 cm in islands (7.1 ± 1.6%) compared to plantations (3.1 ± 0.9%, $F = 5.4$, $p = 0.0397$). The percent of seedlings with decreasing height varied significantly by species ($F = 7.4$, $p = 0.0007$, *Terminalia* 9.4 ± 2.3%, *Vochysia* 1.2 ± 0.5%, *Erythrina* 6.9 ± 2.3%, *Inga* 2.0 ± 1.3%); there were no site or interaction effects ($p > 0.05$ in all cases).

Seedling height changed minimally the first year and then increased considerably in the second and third years (Fig. 2b)
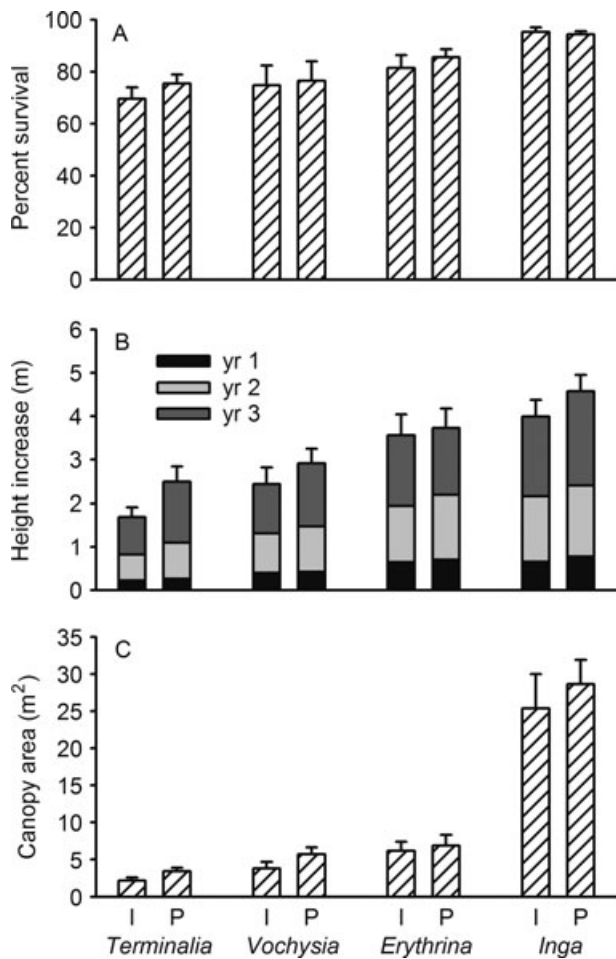
Figure 2. Percent survival (a), height increase (b), and canopy area (c) after 3 years in island (I) and plantation (P) treatments for four species. Error bars indicate 1 SE.

Table 2. Mixed-model ANOVA of the effect of site, species, and planting design (PD) on height change and canopy area in year 3.

	Height Change			Canopy Area		
Factor	*F*	*df*	*p*	*F*	*df*	*p.*
Site	6.8	11	<0.0001	5.7	10	0.0003
PD	7.8	1	0.0174	9.6	1	0.0113
Species	29.7	3	<0.0001	83.3	3	<0.0001
Species*PD	2.6	3	0.0692	2.9	3	0.0498
Species*Site	4.8	31	<0.0001	4.4	29	<0.0001
Site*PD	4.8	11	0.0003	4.2	10	0.0013

growing approximately 2–4 m over the 3-year period. Site, species, planting design (PD), and the species × PD and site × PD interactions all significantly affected seedling height increase (Table 2). Height increased across species in the following order *Terminalia* < *Vochysia* < *Erythrina* < *Inga* (Fig. 2b). At seven sites, seedlings growth was >0.75 m more in plantations than islands, at three sites there was essentially
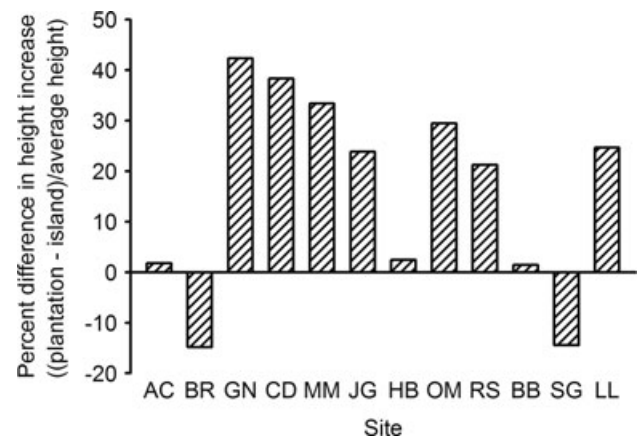

Figure 3. Percent difference in height increase (∆ height in plantation − ∆ height in island)/∆ height in both planting designs) for all species averaged across 12 sites. A positive value on the *y*-axis indicates greater growth in the plantations and a negative value indicates greater growth in the islands. Sites are ordered according to increasing overall height increase. See Table 1 for site descriptions.

no difference, and at two sites seedlings grew slightly more (0.24 m and 0.64 m) in islands (Fig. 3), which explains the significant site × PD effect. Canopy area showed similar trends (Table 2), as height change and canopy area in year 3 were strongly correlated (*Terminalia*: $r = 0.92$, *Vochysia*: $r = 0.93$, *Erythrina*: $r = 0.91$, *Inga*: $r = 0.85$, $p < 0.0001$ for all species). Although height differences were on average within 1–3 m of each other, *Inga* provided 4–10 times more canopy cover than the other species (Fig. 2c).

Height increased 0.26 m more in the plantation interior compared to the edge ($F = 6.4$, $p = 0.0275$) with no significant species × edge/interior (EI) interaction ($F = 0.9$, $p = 0.46$). For canopy area there was a significant species × EI interaction ($F = 3.6$, $p = 0.0246$), but there was no significant EI effect ($F = 0.8$, $p = 0.3905$) as only *Inga* had higher canopy area in the interior. Neither survival nor height change of all species in small/medium versus large islands differed significantly ($t < 1.5$, $p > 0.15$ in all cases).

Soil and Foliar Nutrients

Soils were moderately acidic with high organic matter and low P (Table 3; Appendix S1). Soil nutrients did not differ between islands and plantations ($t < 1.8$, $p > 0.05$ in all cases). Several soil properties had a 2-fold or greater variation across sites, including bulk density, organic matter, N, C, P, CEC, and most micronutrients.

Foliar nutrient concentrations were not significantly different between planting designs ($F < 3.8$, $p > 0.05$), but they always differed significantly by species (Table 4; Appendix S2). The two N-fixers, *Inga* and *Erythrina*, had higher foliar N. *Erythrina* also had higher foliar P, K, and S. *Vochysia*, which sequesters Al, had foliar values >25 times higher than other species. The only soil nutrient that was consistently linked to foliar nutrients was P; foliar P was correlated with

Table 3. Soil nutrients. Values are means ± SE and minimum and maximum values for all plots ($n = 24$ plots, 12 islands, and 12 plantations).

Soil Variable	Mean ± SE (Min–Max)
Bulk density (g cm^{-3})	0.607 ± 0.020 (0.42–0.78)
pH	5.52 ± 0.04 (5.1–5.9)
Organic matter (%)	15.67 ± 0.99 (9.1–22.7)
N (%)	0.60 ± 0.04 (0.3–0.9)
C (%)	7.46 ± 0.57 (3.4–12.5)
C:N	12.2 ± 0.2 (10.2–14.0)
Bray P (mg kg^{-1})	15.3 ± 0.9 (10–30)
Mehlich III P (mg kg^{-1})	4.5 ± 0.5 (2–11)
CEC (me 100 g^{-1})	14.53 ± 1.62 (4.8–37.8)
K (mg kg^{-1})	183.3 ± 28.0 (59–641)
Ca (mg kg^{-1})	1384.3 ± 181.0 (370–3903)
Mg (mg kg^{-1})	233.2 ± 28.2 (90–646)
Na (mg kg^{-1})	36.9 ± 0.6 (30–43)
Al (mg kg^{-1})	1617.2 ± 46.3 (1104–2204)
Fe (mg kg^{-1})	51.8 ± 5.3 (21–129)
Mn (mg kg^{-1})	22.5 ± 3.5 (5–65)
Cu (mg kg^{-1})	5.6 ± 0.3 (2–8)
Zn (mg kg^{-1})	2.8 ± 0.7 (1–15)

Values are from soil samples taken at 0–15 cm except bulk density which was taken at 0–10 cm. CEC, cation exchange capacity.

Bray soil P for all three species (*Terminalia* $r = 0.55$, $p = 0.0057$, *Vochysia* $r = 0.46$, $p = 0.0235$, *Erythrina* $r = 0.42$, $p = 0.0386$, *Inga* $r = 0.28$, $p = 0.1811$).

Foliar and soil nutrients potentially influenced tree growth in a few cases. Height change (HC) and canopy area (CA) for *Terminalia* were significantly correlated with foliar N (HC: $r = 0.67$, $p = 0.0003$; CA: $r = 0.72$, $p = 0.0002$); likewise, *Vochysia* growth was marginally correlated with foliar N after correcting for multiple comparisons (HC: $r = 0.51$, $p = 0.0215$; CA: $r = 0.60$, $p = 0.0050$; corrected significance level is $p < 0.0048$). Soil Cu was significantly correlated with growth in three species (*Terminalia* HC $r = 0.59$, $p = 0.0025$; *Erythrina* HC $r = 0.60$, $p = 0.0018$; *Vochysia* CA $r = 0.65$, $p = 0.0018$). *Terminalia* height change and canopy area were also significantly correlated with foliar S (HC: $r = 0.64$, $p = 0.0008$; CA: $r = 0.62$, $p = 0.0022$), and *Vochysia* canopy area was correlated with foliar B ($r = 0.64$, $p = 0.0065$). No other soil or foliar nutrients were significantly correlated with height change and canopy area (within the same species) after adjusting for multiple comparisons. However, foliar N in the two non-N-fixing species (*Terminalia* and *Vochysia*) was strongly correlated with canopy area for *Inga* (*Terminalia*: $r = 0.76$, $p < 0.0001$ *Vochysia*: $r = 0.67$, $p = 0.0007$); in other words when *Inga* grew well, so did *Terminalia* and *Vochysia*.

Plant Physiological Responses

LMA was higher in islands than plantations ($F = 4.8$, $p = 0.0305$), whereas leaf level photosynthesis did not differ across treatments (Table 5). Among species, *Inga* had the highest photosynthetic rates on an area basis and *Vochysia* had the lowest (Table 5). When analyzed on a weight basis, the photosynthetic rate of *Erythrina* was three times higher than the

Table 4. Foliar nutrients by species. Values are means ± SE and minimum and maximum values ($n = 24$ plots, 12 islands, and 12 plantations).

Nutrient	Terminalia	Vochysia	Erythrina	Inga
N (%)	1.88 ± 0.08[a] (1.3–3.1)	1.74 ± 0.06[a] (1.3–2.2)	4.27 ± 0.10[b] (2.7–4.8)	3.12 ± 0.08[c] (2.5–4.3)
P (%)	0.151 ± 0.013[b] (0.09–0.34)	0.107 ± 0.007[a] (0.08–0.27)	0.263 ± 0.011[c] (0.11–0.34)	0.157 ± 0.005[b] (0.10–0.20)
K (%)	0.72 ± 0.02[a] (0.5–0.9)	0.68 ± 0.03[ab] (0.5–1.2)	1.57 ± 0.07[b] (0.8–2.2)	0.80 ± 0.02[a] (0.6–1.1)
Ca (%)	1.32 ± 0.06[a] (0.6–2.0)	1.26 ± 0.04[ab] (0.7–1.7)	1.22 ± 0.07[ab] (0.5–2.0)	1.07 ± 0.05[b] (0.6–1.7)
Mg (%)	0.239 ± 0.013[b] (0.14–0.38)	0.330 ± 0.016[a] (0.21–0.48)	0.365 ± 0.021[a] (0.13–0.55)	0.159 ± 0.011[c] (0.10–0.37)
S (%)	0.125 ± 0.004[a] (0.09–0.16)	0.178 ± 0.007[b] (0.12–0.25)	0.230 ± 0.006[c] (0.16–0.28)	0.166 ± 0.005[b] (0.12–0.23)
B (mg kg^{-1})	45.5 ± 3.4[a] (15–88)	31.1 ± 1.6[b] (15–45)	36.7 ± 2.4[b] (20–60)	31.9 ± 2.0[b] (17–54)
Al (mg kg^{-1})	265.2 ± 24.8[c] (49–658)	23106.8 ± 654.7[d] (17140–28729)	795.0 ± 97.4[b] (91–2217)	181.6 ± 19.9[a] (39–508)
Fe (mg kg^{-1})	74.2 ± 8.0[ab] (33–178)	61.6 ± 12.1[a] (30–329)	104.6 ± 6.6[b] (54–216)	93.1 ± 6.9[ab] (49–192)
Mn (mg kg^{-1})	172.4 ± 17.6[a] (71–436)	169.9 ± 11.8[a] (81–314)	124.8 ± 6.7[b] (57–193)	165.2 ± 18.1[a] (59–357)
Cu (mg kg^{-1})	13.2 ± 0.9[b] (7–22)	9.1 ± 0.9[a] (5–20)	14.0 ± 1.0[b] (9–27)	15.7 ± 1.0[c] (10–28)
Zn (mg kg^{-1})	27.6 ± 1.9[a] (17–62)	18.4 ± 1.2[b] (13–40)	29.8 ± 1.1[a] (17–38)	20.4 ± 0.6[b] (16–26)

Means with the same letter within a row are not significantly different ($p > 0.05$) using Tukey's mean separation procedure.

Table 5. Physiological and morphological values by planting design and species.

Factor	Area Based A_{max}	Weight Based A_{max}	LMA	PNUE	PPUE
Planting Design					
Island	12.4 ± 0.7	162.7 ± 18.9	87.8 ± 5.2*	62.4 ± 3.5	1011.0 ± 8.2*
Plantation	12.6 ± 0.7	193.6 ± 19.1	73.5 ± 5.3	79.5 ± 8.2	1315.3 ± 101.2
Species					
Inga	15.3 ± 0.8[a]	166.0 ± 0.6[b]	93.7 ± 3.7[a]	56.2 ± 4.6[b]	1136.5 ± 130.5[ab]
Erythrina	13.9 ± 0.9[ab]	310.9 ± 23.4[a]	42.3 ± 2.8[b]	88.8 ± 14.4[a]	1354.0 ± 143.8[a]
Terminalia	11.8 ± 0.7[bc]	129.5 ± 12.5[b]	96.4 ± 6.9[a]	72.3 ± 7.9[b]	993.5 ± 138.3[b]
Vochysia	9.4 ± 0.5[c]	116.2 ± 9.8[a]	84.4 ± 5.3[a]	66.9 ± 5.5[b]	1182.3 ± 93.9[b]

Values are means $\pm$ SE for ($n = 4$/species/site). * denotes a significant planting design effect. Species with the same letter are not significantly different ($p > 0.05$) using Tukey's mean separation procedure. A_{max}, maximum net CO_2 assimilation by area (μmol m^{-2} s^{-1}) and by weight (nmol g^{-1} s^{-1}); LMA, leaf mass per unit area (g m^{-2}); PNUE, photosynthetic nitrogen use efficiency; PPUE, photosynthetic phosphorus-use efficiency (nmol CO_2 s^{-1} mol nutrient^{-1}).

other species, which is related to its low LMA (Table 5). *Inga* had the highest light saturation point and the lowest light compensation point (data not shown), consistent its rapid growth. *Vochysia* had the lowest maximum photosynthesis, and photosynthesized efficiently across the narrowest range of light levels. Both photosynthetic N and P use efficiency (PNUE and PPUE) were relatively site specific with significant site × treatment interactions (Table 5, PNUE: $F = 7.0$, $p = 0.0022$, PPUE: $F = 7.1$, $p = 0.0021$). PPUE was higher in plantations ($F = 13.6$, $p = 0.0027$), whereas PNUE did not differ by planting design ($F = 3.2$, $p = 0.0980$). *Erythrina* had higher PNUE and PPUE than other species (PNUE: $F = 19.4$, $p < 0.0001$; PPUE: $F = 3.6$, $p = 0.0431$).

Discussion

Planting Design

To our knowledge, this is the first study to compare survival and growth of seedlings in different planting designs to facilitate tropical forest recovery. Although planting tree islands has been proposed as a cheaper forest restoration strategy that better simulates natural recovery (Robinson & Handel 2000; Zahawi & Augspurger 2006; Rey Benayas et al. 2008), our results show both positive and negatives aspects of this planting approach.

At most sites, seedlings grew more in plantations, which cannot be explained by differential competition with ruderal herbaceous and shrub species, as these plants were cleared for the first 2.5 years of the study. There are two possible explanations for this unanticipated result. First, the majority of seedlings planted in islands are near an edge where abiotic conditions may be more stressful. In fact, seedlings increased slightly more in height in plantation interiors than at edges, possibly due to reduced shade at edges. Past studies have shown that tropical seedlings can experience photoinhibition at high light levels (Krause et al. 1995; Loik & Holl 2001; dos Santos et al. 2006), particularly when their light saturation point is relatively low, as for *Terminalia* and *Vochysia*. We recorded higher LMA in islands which suggests more allocation to leaf mass in response to higher light levels.

Second, because the outer rows in both plantations and islands are non-N-fixers, N-fixers comprise a larger proportion of plantations (46%) compared to islands (33%), which likely facilitated growth of *Terminalia* and *Vochysia*. The higher density of N-fixers may explain higher PPUE in plantations, due to the large P demand of N-fixers (Dommergues 1995; Siddique et al. 2008). In another study, Cole (unpublished data) found that later-successional tree seedlings accumulated greater biomass in the plantations than in 8- to 10-year-old secondary forests with few N-fixing trees. Moreover, other studies show that interplanting fast growing, N-fixers, particularly *Inga edulis*, enhance growth and foliar nutrients of other species (Carpenter et al. 2004b; Nichols & Carpenter 2006; Siddique et al. 2008). Given that planting design and density of N-fixers were confounded it is impossible to tease out the two effects.

Whereas seedling survival was similar in islands and plantations, more seedlings decreased in height in islands, due partly to the higher frequency of damage incurred during ruderal vegetation clearing (Holl & Zahawi, authors' personal observations). Due to the less uniform planting arrangement, workers found it more difficult to locate island edges in the grass, despite the fact that the workers were well trained in the clearing methodology and all seedlings were marked with 0.5-m bamboo stakes and flagging tape. To avoid this problem, taller marking posts ($\geq$1 m) could be used or ruderal vegetation could be cleared more frequently to improve seedling visibility, but these would both increase costs.

Despite higher overall growth and potentially less maintenance-related damage in plantations, the benefits of the island planting strategy compare favorably in terms of costs. In our case, we planted approximately 27% the number of seedlings in islands compared to plantations, which reduces planting and maintenance costs by a similar percentage. These costs are considerable (for a seedling density of 3 × 3 m, typical for forestry in the region, planting = $400 - 600 ha^{-1}, maintenance = $500 - 700 ha^{-1}yr^{-1}; Zahawi & Holl 2009). The cost of replanting the approximately 4% damaged seedlings in islands is relatively minor in comparison. The overall height difference between plantation and island plots in our study was 0.6 m over 3 years, which is roughly equivalent to 0.5 years of growth; so it may be necessary to clear

longer in island plots, but this would be substantially cheaper than planting the entire area.

Survival and growth did not differ among island sizes, although the strength of our comparisons was compromised by small seedling numbers. Larger islands may be more practical, however. First, the smaller the island the greater the impact if one or two seedlings die. Second, larger islands are easier to locate when clearing ruderal vegetation. Moreover, related research shows that larger islands receive more bird visitations (Fink et al. 2009) and animal-dispersed seed rain (Zahawi & Augspurger 2006; Cole et al. 2010).

Species-Specific Differences

To increase the applicability of our study, we selected species that are widely used for reforestation and agroforestry in Central America (Butterfield & Espinoza 1995; Carpenter et al. 2004a; Calvo-Alvarado et al. 2007) and survival rates were accordingly high. *Inga edulis* is particularly well suited for restoration due to rapid canopy development, which provides shade, favorable microclimatic conditions, and the potential for animal use (Pennington & Fernandes 1998; Fink et al. 2009). Both growth and physiological measurements its ability to survive and grow under a range of light conditions, whereas our and other studies show that *Inga* enhances growth of other species (Carpenter et al. 2004b; Nichols & Carpenter 2006). *Erythrina poeppigiana* generally has high productivity and a fast leaf turnover rate and is efficient at taking up N and P, as indicated by its PNUE and PPUE and the correlation between foliar P and height growth. *Erythrina* can be propagated vegetatively to develop considerable canopy cover in a short time frame (Zahawi & Holl 2009). It produces a relatively sparse canopy and is frequently attacked by herbivores (Araya et al. 1992), however, compromising its value for restoration. *Erythrina poeppigiana* and *Inga edulis* are native to northwestern South America, although both are ubiquitous as shade trees in Central American agricultural landscapes. This raises the question of whether these species should be used for restoration, and other species within these genera merit testing. Although *Terminalia amazonia* and *Vochysia guatemalensis* have lower photosynthesis rates and, therefore, close canopy later, they have been used successfully in numerous forestry projects (Butterfield & Espinoza 1995; Piotto et al. 2003; Calvo-Alvarado et al. 2007).

Site-Specific Differences in Seedling Growth and Nutrients

Strong site-specific differences are a common result of the few studies conducted at several sites (Calvo-Alvarado et al. 2007; Wishnie et al. 2007) and highlight the need to replicate at multiple sites to draw general ecological conclusions and make restoration recommendations (Hurlbert 1984; Hayes & Holl 2003). For example, we found 3- to 4-fold differences in height of all species among sites. Moreover, we recorded higher growth in plantations at most but not all sites. If we only add data from one or two sites with contrasting results, our conclusions would have been quite different.

Sites varied considerably in nutrient levels and soil compaction. Average bulk density was similar to values reported for abandoned pasture or primary forest in Costa Rica (Reiners et al. 1994; Holl 1999; Krishnaswamy & Richter 2002), but varied by almost 2-fold among sites. Total soil N also was comparable to other studies in both primary forests (Reiners et al. 1994; Cleveland et al. 2003) and plantations (Nichols et al. 1997; Powers et al. 2005). In contrast to past tropical forestry studies (e.g. Nichols et al. 1997; Herrera et al. 1999), in only a few cases did differences in soil nutrients or compaction explain a substantial amount of the variation in growth. *Terminalia* and *Vochysia* growth were correlated to foliar N, consistent with other reforestation studies showing that foliar N is a good predictor of growth (Craven et al. 2007). For three species either height increase or canopy area were positively correlated to soil Cu (see also Davies 1997; Herrera et al. 1999), which may reflect the role that Cu plays in lignin formation (Goransson 1998). *Terminalia* growth was also related to foliar sulfur, which is often a limiting element in tropical soils (Pasricha & Fox 1993).

Surprisingly, we did not find a relationship with soil P as volcanic soils are commonly P limited (Uehara & Gillman 1981; Vitousek 1984). From an agricultural perspective, these soils are very low in available P, but our values are only slightly less than a nearby site (Nichols et al. 1997) and several other sites in the neotropics (Powers et al. 2005). Labile P, as well as most soil nutrients, vary a great deal temporally and spatially (Vitousek & Sanford 1986; Townsend et al. 2008), and our one-time, plot level measurement may have been insufficient to discern relationships. It is also likely that seedling growth was influenced by differences in mycorrhizal and other microbial communities (Carpenter et al. 2001; Allen et al. 2003; Aldrich-Wolfe 2007).

Concluding Thoughts

Our results show advantages (good seedling survival, cheaper) and disadvantages (more damage to seedlings, slightly lower growth) in using an island planting design. Ultimately, the effectiveness of this strategy will depend on how quickly islands spread and facilitate the establishment of forest species over time. To date the islands have expanded 0–3 m, principally due to spread of the planted tree canopy rather than to recruitment and growth of successional vegetation at this early stage in the study (Zahawi & Holl unpublished data). Island plantings may result in a species composition more similar to the surrounding forest due to a lesser influence of the planted trees on long-term species composition, particularly given the strong signal of the high density of N-fixing species in our plantings. Moreover, over time the dense shade of the N-fixers may inhibit the survival and growth of some species, so the more heterogeneous islands may actually facilitate the recovery of a more diverse suite of species.

Most landowners are interested in planting commercially valuable species on their properties. Our results, however, show that from a restoration perspective interplanting fast-growing species with slower-growing, timber-valuable species

quickly provides canopy cover which encourages seed dispersers, shades out ruderal vegetation, and should facilitate forest recovery.

Implications for Practice

- Planting patches (islands) of trees provides a lower cost option for restoring large areas of tropical forest, but our results suggest some tradeoffs to this restoration strategy, including slightly lower growth rates and potential damage to seedlings due to the irregular planting design.
- Interplanting fast-growing, N-fixing species helps improve growth of slower-growing commercially valuable species and provide rapid canopy cover to facilitate natural establishment of other species.
- Given high intersite variation, replicating restoration projects at several sites is critical to making general management recommendations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Soil nutrient data for all plots.
Appendix S2. Foliar nutrient data for each species at each site.

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